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Tracks, Trai ls and Trampling by Large Vertebrates in a Rif t Valley Paleo-Wetland, Lowermost Bed II, Old uvai Gorge, Tanzania

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The impact of large vertebrates on the seclin1entary record in an East African groundwater-fed wetland in Ngorongoro Crate1; Tanzania, is used as a modern analog to interpret an ancient (Plio-Pleistocene) wetland record in Olduvai Gorge, Tanzania. The 3 km^2 wetland at Olduvai is characterized by n1assive silty claystones produced by intense vertebrate trampling, as well as trails by vertebrates frequenting the wetlands and isolated footprints that represent a "snapshot in time." Based on n1odern analogs, a paleo hippo trail (1.2 1n \vide and 0.6 m deep) in the PHo-Pleistocene wetlands is interpreted as a frequently used corridor between hippo pools (days) and grazing n1eado\YS (nights),

Groundwater-fed wetlands are low energy environments where the physical record appears to be dominated by plant and animal activity. The bioturbation record reflects a number of interacting factors such as substrate texture, 1noisture content ,sedimentation i·ate, frequency of flooding, type of animals 11resent, trantpling rate, and post-depositional changes (co1npaction). Lithofacies in both the ntodern and ancient "wetlands include ntuddy sandstone (drainage channels) and silty claystone (vegetated and nonvegetated mud flats). Organic-rich sedin1ents eventually oxidize, eliminating most evidence of the habitat. modern \vetlands have organic-rich n1ud and peat, whereas the ancient analog has siliceous earthy claystones that contains plant rentains, bone fragn1ents, pollen, phytoliths, and localized beds of diatomite. Thus, the physical record of vertebrate bioturbation in conjunction \\ith paleontological and lithological records provides crucial information on the ecology of ancient "\\'Ctland environ1nents.

Keywords hippo trail, tran1pling, paleo-wetland, Olduvai Gorge

INTRODUCTION

Groundwater-fed wetlands may occur in any lo\v ground (lake margins, river flood plains and deltas), basically wherever the water table intersects the surface. Wetlands are also associated with impervious materials (perched groundwater) or linked to geological structures (faults or bedrock systems) that are natural conduits for flo\v. Thus, in certain geological contexts wetlands may be small isolated features and occur separately and distinct from major water bodies. Freshwater wetland records have been neglected as a focus of study, particularly in arid and semi-arid environments, despite the fact that they are and have been important ecologically as a water resource (Ashley, 2001). Arid to semi-arid environments receive 500-1000 mm precipitation annually but can experience 2000-3000 mm annual evaporation. The logical affinity of fauna -to dependable, potable \water suggests that \wider recognition of ancient wetland deposits could lead to discove1y of previously overlooked paleontological records.

The multiplicity of geological settings in which wetlands occur creates a variety of depositional contexts for \wetlands, and yet there is a dearth of basic description of their distinctive seditnentological record. There are several reasons why groundwater-related environments have not been \widely recognized.

1. There is a misconception that ground\vater discharge always produces travertine and sinter deposits. Many springs and groundwater seeps, particularly cool ones (<30°C), have little to no associated mineral deposits (Quade et al., 1995; Deocampo, 2001).
2. Most spring deposits are restricted in size (few m^2) and thus could be overlooked during fieldwork.
3. Preservation potential of wetland peats and organic-rich sediments is low. Organic-rich seditnent oxidizes \with time, unless preserved in an acidic (<5.5 pH), anoxic environment (Thompson and Hamilton, 1983; Quade et al., 1998).
4. Some ancient ground\water-fed \wetland deposits have been misinterpreted as floodplains, deltas, or marshy fringes of lakes (Hay, 1976). However, the location of rivers and lakes can shift laterally with time, whereas

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groundwater-fed wetlands that are controlled by topography or underlying geology are expected to maintain a relatively fixed location.

A large interdisciplinary research effort, OLAPP (Olduvai Landscape Paleoanthropology Project), to reconstruct a Plio-Pleistocene landscape (-25 km wide) spanning a nmmw window of time (-50 ka) (Blumenschine and Masao, 1991), provided an excellent opportunity to study a paleo wetland. Geologic mapping and sedimentologic description provided the basis of paleoenviron1nenta 1 reconstruction of a number of Plio-Pleistocene deposits within the paleontologically rich Olduvai Gorge, Tanzania, which included alluvial fan, fluvial plain, lake margin, ephemeral stream, and playa lake, in addition to a large wetland (Ashley and Hay, 2002) (Fig. 1). The wetland was 3 km^2 and appears to have been mainly groundwater-fed (Ashley, 1996; Liutkus, 2000; Ashley, 2001; Deocampo, 2002a). Results from the archaeological and paleontological studies will be reported elsewhere.

The wetland deposit is characterized by vertebrate bioturbation that yielded structureless silty and earthy claystones, distinct trails of superimposed tracks, and isolated footprints. Although vertebrate bioturbation has been recognized previously as an itnportant process, the paleoenviron1nental inte1pretations \Vere associated \Vith sedimentation in depositional systen1s such as volcaniclastic (Leakey and Hay, 1979), lake margin (Laporte and Behrensmeyer, 1980; Renaut et al., 1986; Hay et al., 1986; Cohen et al., 1993; Deocampo and Ashley, 1999), fluvial (Haynes, 1985; Holliday, 1995), deltaic (Behrensmeyer and Laporte, 1981), and coastal (Van der Lingen and Andrews, 1969) environments. There is now a need to extend the docu1nentation of bioturbation to groundwater-fed wetland systems.

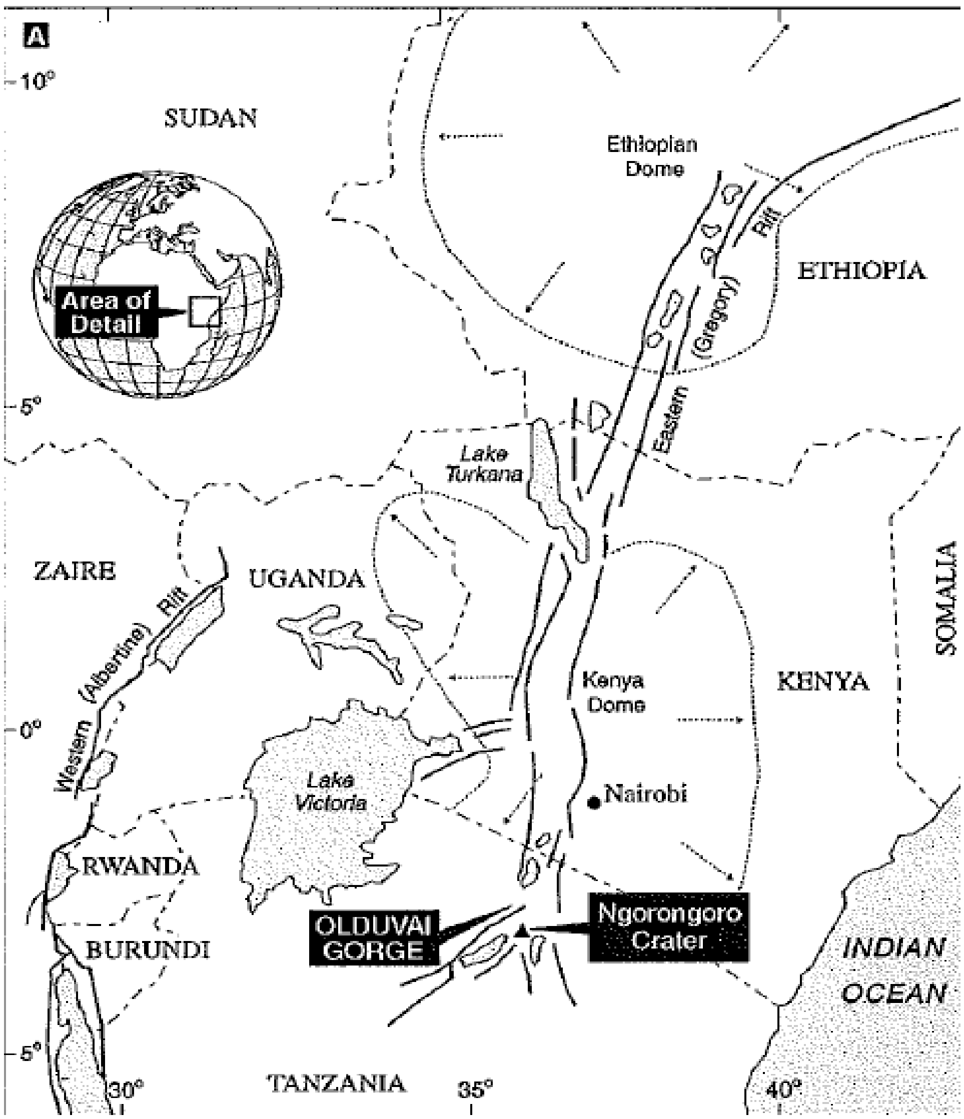


FIG. 1. A regional location map of the Eastern (Gregory) and \Vestern (Albertine) rifts in East Africa depicts the location of Olduvai Gorge on the west 1nargin of the Eastern rift and Ngorongoro Crater at a bifurcation of the rift, both in northern Tanzania.

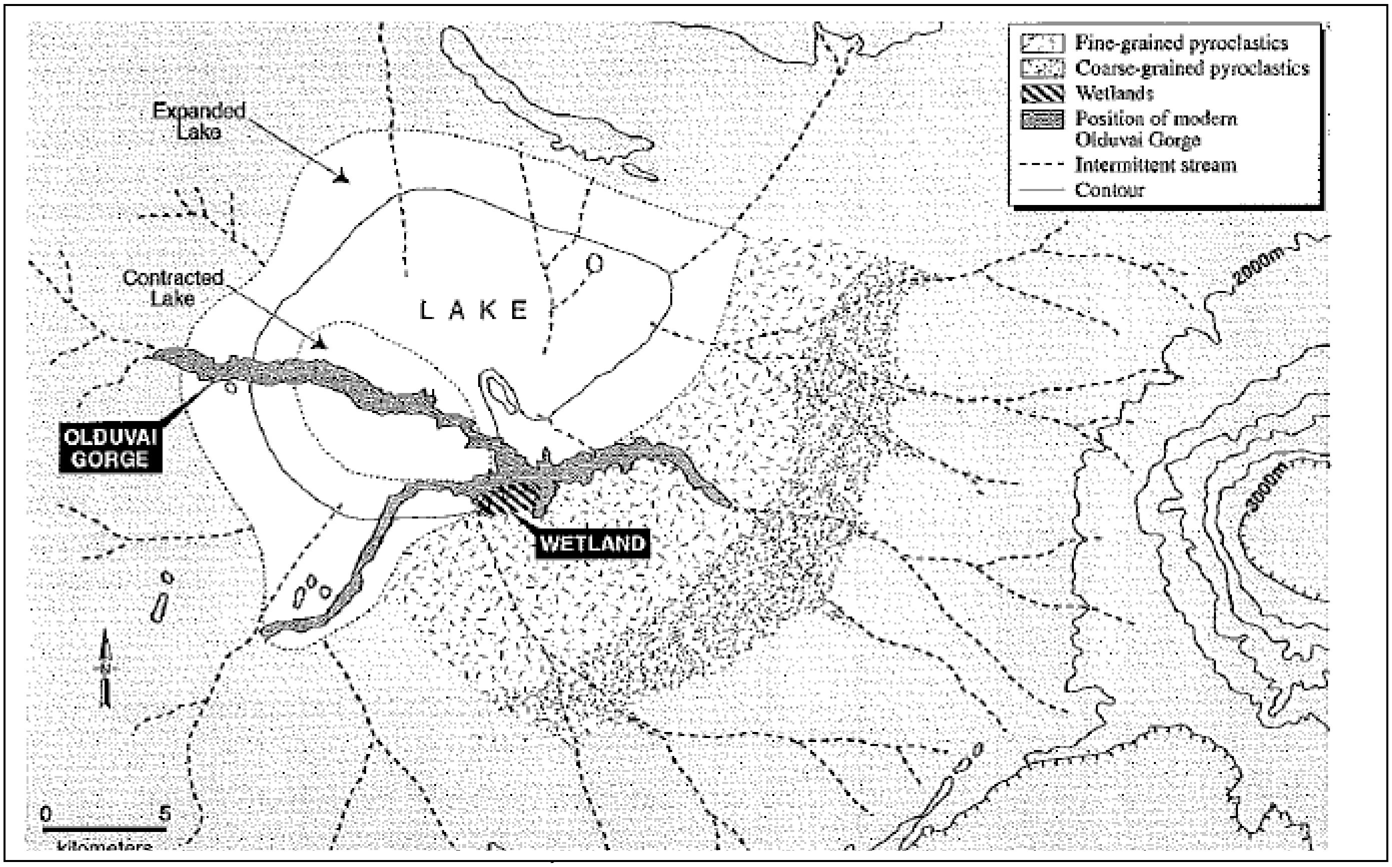


FIG. 2. Paleogeographical reconstn1ction of the Olduvai Basin during early Pleistocene time (modified from Hay, 1976). The area covered during Jake expansions and the location of the groundwater-fed \Vetland that deYeloped on the southeastern margin of the lake are depicted. The outline of the 1nodern Olduvai Gorge is shown for reference.

The objectives of this paper are to: (I) summarize the geologic and sedimentologic context of groundwater-fed wetland deposits in a semi-arid setting based on observations fro1n an ancient and a 1nodern environ1nent, (2) describe the characteristic bedding and structures formed by vertebrate reworking of the substrate, and (3) discuss preservation potential of large terrestrial manunal bioturbation that is relatively con1mon in the 1nodern environment, but rarely recognized in the geologica1 record.

GEOLOGICAL SETTING

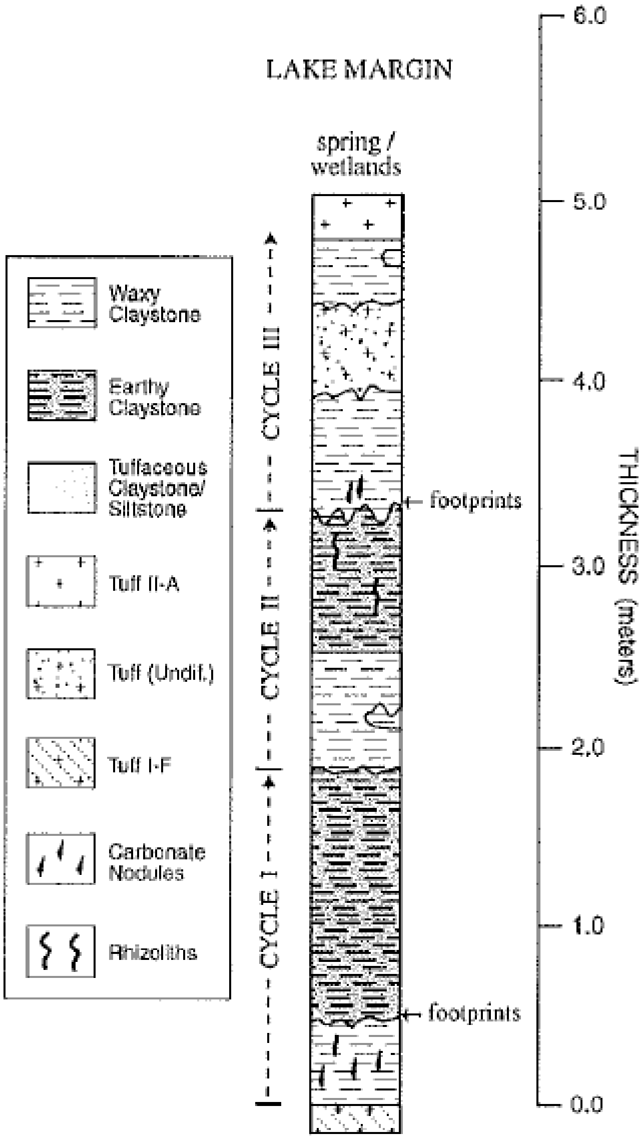
Modern Wetlands, Ngorongoro Crater

Ngorongoro Crater is the caldera of a large trachytic volcano 1ocated in the East African Rift, northern Tanzania, about 40 kln from Olduvai Gorge, and provides a good modern analog for ancient groundwater-fed wetlands (Deocampo and Ashley, 1997; Deocampo and Ashley, 1999) (Fig. I). The caldera collapsed approximately t\VO n1illion years ago creating an internally drained basin, 23 km wide at the top and ca. 15 km in diameter in the "crater" bottom. About 20,000 large animals use the area for food and water. The lake in the center of the ca1dera has varied in size and che1nistry since the late Pleistocene and at present is best described as a playa (Pickering, 1965; Hay, 1976; Deocampo, 2001). Two perennial rivers drain into the caldera, and many active springs are scattered throughout the basin. These areas of groundwater discharge support extensive wetlands and provide potable water for thousands of animals daily (Estes and Small, 1981).

The spring-wetland site used in this study, Mti Moja, is a persistent ground\vater source located in the center of the caldera. Freshwater flows from the spring orifice over nearly one kilometer; gradually evaporating to a brine (Deocampo and Ashley, 1999; Deocampo, 2001). A ca. 10,000 m^2 wetland occurs in the freshest part near the spring and is a well-established habitat for hippos (Deocampo, 2002b). The wetland has a spring drainage channel caITying low velocity flows and pools of standing water (excavated by the hippos). Other subenvironments include marsh as \Ve11 as vegetated and unvegetated 1nud flats. A black rhino calving ground is nearby on slightly higher ground.

Plio-Pleistocene Wetlands, Olduvai Gorge

Olduvai Gorge is an incised river valley draining from the eastern Serengeti Plain toward the Eastern Rift valley (Fig. 1). The Gorge exposes a t\vo-1ni1lion year record across a 50



I•IG. 3. A representative stratigraphic section (ca. 5 m thick and 1 m wide) fron1 the early Pleistocene lake-margin wetlands, Olduvai Gorge, is comprised of tuft's and interbedded claystones: green smectitic claystone deposited in a saline-alkaline lake and siliceous "earthy" claystone deposited in the groundwater-fed wetlands. The bedding contacts are lithologically sharp, but are comn1only irregular and undulating; these surfaces are interpreted as having been bioturbatcd by large animals frequenting the wetlands.

kilometer-wide rift-platform sedimentary basin that was located on the western margin of the main rift valley (Ashley and Hay, 2002). The shallow sedimentary basin was situated between Precambrian basement (west) and the Plio-Pleistocene Ngorongoro Volcanic Highland (east). The basin fill, that is now disrupted by rift-parallel faults, is thin (100 m), and comprised of interbedded primary aitfall tuffs, reworked volcaniclastic sediments, and locally quartzo-feldspathic sediments (Hay, 1976).

Paleoenvironmental reconstruction of a short (-50 kyr) interval of time starting at -1.75 Ma revealed a semi-arid landscape within a closed depression (Hay, 1976, 1990; Ashley, 2000). The interval is recorded as a 6-m thick sedimentary deposit that is dominated by a saline-alkaline playa lake that fluctuated episodically over several square kilometers of the lake margin (Figs. 2, 3). A 3 km^2 spring and wetland complex was identified near the base of the adjacent Ngorongoro Volcanic Highland (Ashley, 1996; Deocampo and Ashley, 1999). In addition to pyroclastic airfoil from Ngorongoro, sediments were transpo1ted into the basin by both \wind and intermittent runoff (rivers and mudflows).

The groundwater-fed spring and wetland complex is adjacent to the lake, sometimes physically separated from the lake and sometimes inundated by it. Lake level changes were likely driven by both short-term (seasonal to decades) and longer-

(Ashley and Driese, 2000). The sedimentary record contains a rich fauna! and cultural record of early Plio-Pleistocene ve1te-

1991).

SEDIMENTOLOGICAL PROCESSES AND LITHOFACI ES

Modern Wetlands, Ngorongoro Crater

The wetland vegetation varies with depth of water, duration of inundation, and salinity. But, ephemeral wet meadows co1n-1nonly have Cynodon, the marsh contains *Scirpus* and *CyJJerus*

Sediments are fine-grained, organic-rich, 10--20% loss-on-ignition (LOI), silty to sandy clays. They are composed of aluminous clays and biogenic a1norphous silica, as \Vell as abundant plant remains (localized root mat and peats) (Deocampo, in press). Occasiona11y a track of a single animal is preserved (e.g., Fig. 4A), but typically the muds are heavily pummeled by foot traffic (e.g., Fig. 4B, C).

Additional lithofacies forming in the modern sedimentary environment range from carbonate (springhead deposit) to muddy sand (spring drainage channel) to silty and alkaline clay (evaporative mudflats and playa lake) to very sandy muds (subaerial sedimentation). The coarse fraction is probably eolian detritus sourced from deflation of adjacent de-vegetated areas. Sands are a 1nixture of tuffaceous minerals, weathered lithic fragments of locally derived lava and Pleistocene carbonates, as well as reworked diagenetic lacustrine calcite. In freshly desiccated areas of the playa lake margin, efflorescent crusts of trona and halite are common, although these are rapidly rewmked by bioturbation and wind. Clays are generally illitic with minor smectite interstratification, with Mg-s1nectite, consistent with diagenesis under saline-alkaline conditions (Hay, 1976; Deocampo, 2001).

Modern Bioturbators

The majority of large vertebrates utilizing the spring/wetland complex, at least seasonally as a water source, are ungulates (wildebeest, black rhinos, gazelles, wart hogs, buffalo, zebras) and elephants (Estes and Small, 1981). Carnivores (lions,

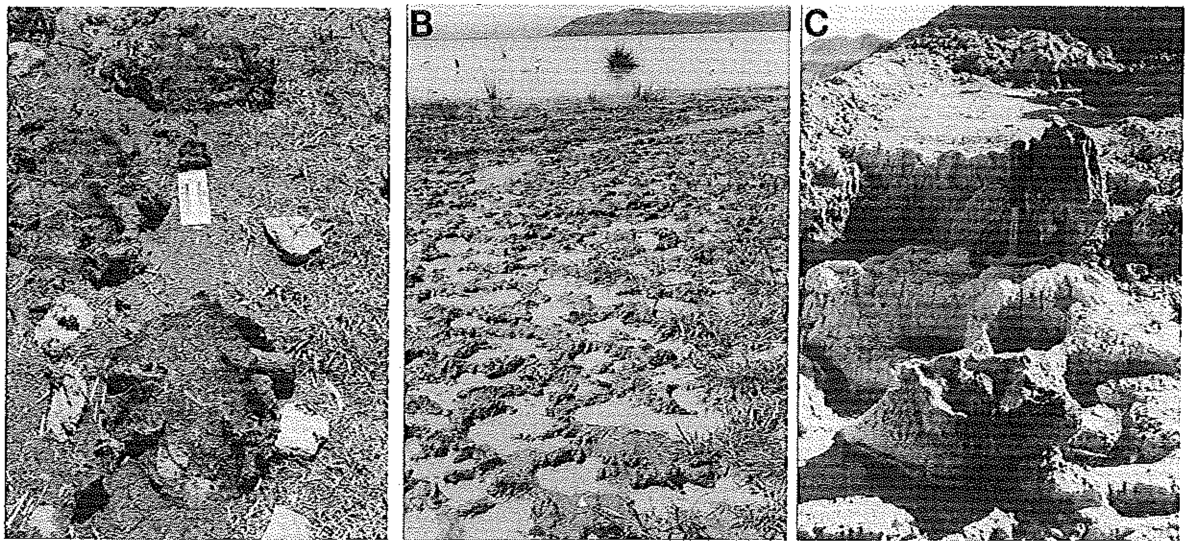


FIG. 4. A. Lake Baringo, Kenya. Tracks of a single hippo moving fron1 top to bottom of photo. The manus (front) print is modified by the pes (hind) print. Substrate is a moderately moist, silty claystone. \Vidth of individual prints ranges from 2529 cm. Length of stride is ca. 100 cm. Scale is 4 cm. Il. Hippo habitat. Intensely bioturbated 1nudflat, \\'ith 1ninor vegetative cover. Substrate is a saturated, silty to sandy 1nud. This n1odern n1udflat is a reasonable analog for ancient deposits in C. C. Early-Pleistocene record, Olduvai Gorge. Bedding plane surfaces at top of siliceous "earthy" claystones con11nonly reveal footprints of large vertebrates. (See Color Plate 1 at the end of this issue).

hyenas, vultures, jackals, etc.) may also frequent the area. Hippos *(Hippopotamus amphibious* Linnaeus) are the only large **vertebrate resident. Another potential permanent wetland** dweller is the crocodile *(Crocodilus niloticus* Linnaeus) (Ross, 1989), and although they occur in other groundwater wetland settings in the rift, crocodiles require a larger more stable fresh-**water environtnent than currently exists at Ngorongoro Crater.** The area of standing freshwater (pools) is small, and the adjacent playa lake is relatively dynamic and thus not ecologically dependable on an annual basis (Deocampo, 2002a).

Hippo adults generally weigh between 1000 and *lSOO* kg, but may reach 4000 kg and thus can have significant impact on the substrate (Marshall and Sayer, 1987). An adult hippo eats about 18 kg of grass (dry weight) per day (Lock, 1972). Hippos are semi-aquatic, spending most days partially submerged in pools (S-SO m in diameter) that they often excavate for themselves. They are gregarious and travel in groups to and from grazing sites (Fig. SA). Most vertebrates frequenting the wetlands tend to follow higher ground, except hippos that tend to seek low grounds. Because of this behavior the hippo trails are usually partially filled with water, and the associated sediment is either saturated or very moist (Fig. SB). They plod along the **trail squeezing mud up and out of the depression, creating a** mud levee (Fig. *SC).* Additional sediment is likely excavated **and carried alway on hooves of the animals. At lo\V water lev-**els, the mud levees and mud banks desiccate and crack (Fig. SD). Claystone blocks slide back into the incised trail, and eventually the trail is infilled by mass movement, windblown sediment, and lake sediments brought in by rising playa lake **water.**

Crocodiles are reptiles that live for several decades and grow to *3-S* m, or greater, in length. They frequent the shallows of lakes and marshes, where the shallow water allows for the penetration of sunlight and results in a diverse fauna (Ross, 1989). **These reptiles are mainly nocturnal hunters and spend 111ost of** their day basking in the sun (Ross, 1989). They utilize the wet-**lands for food, as protection from carnivores, and to maintain** thermal stability. Their diet consists of a wide variety of ani-**mals, fro1n frogs, birds, fish, s1nal1 1na1nmals, and insects, to** larger prey such as buffalo, hippos, zebras, antelopes, and wildebeest (Ross, 1989). Although they feed in the wetlands, they nest and lay eggs on slightly higher, better drained te1rnin nearby. Their footprints (Fig. 6A, B) and tail prints (Fig. 6C) **are common in the environs of wetlands that are associated** with stable bodies of standing water.

Plio-Pleistocene, Olduvai Gorge

During low lake levels a large groundwater-fed wetland, fed by precipitation at higher elevations on the Volcanic Highland (>lSOO m above the basin floor), developed on the southeastern margin of the Olduvai basin (Fig. 2). Small springs likely empted along the slope and at the base of a volcaniclastic fan. Localized carbonate deposits composed of masses of micrite (l-3 m^2 in diameter and ca. 30-SO cm thick) record the former presence of springs (Liutkus, 2000). The wetland covered >3 km^2 and is represented by siliceous earthy claystone. Earthy claystones are interbedded with green waxy claystones, interpreted as saline-alkaline lake sediments by Hay (1976). During high lake levels the playa lake covered the wetlands area drowning the marsh. Figure 3 depicts 2-1/2 lake cycles in a rep-

TABLE I

Plio-Pleistocene 4-meter thick paleontological record of interbedded freshwater-wetland and lake sedin1ents, MCK, lowennost Bed II, Olduvai Gorge, Tanzania.

Thickness (111)	Lithology	Environ1nent	Taxon
0.2	Tuff	Subaerial	No fossils
0.2	Reworked-tuff	Subaerial	Manunal, bovid
0.1	waxy claystone	*Lacustrine	Mammal, reptile
0.8	Earthy claystone	Wetland	Manunal, carnivore, suid, equid, bovid, aves
0.3	waxy claystone	*Lacustrine	Reptile, manunal, bovid
0.3	Earthy claystone	Wetland	Aves, bovid, rhino, equid, bovid, mammal
0.7	Tuffaceous claystone	Mud flat	Aves, bovid, hippo, mamn1al
1.0	Earthy claystone	Wetland	Aves, bovid, mamn1al
0.2	waxy claystone Tuff	*Lacustrine	No fossils
0.2		Subaerial	No fossils

Fossil identification by Amy Cushing (Cushing, 2002).

'"Lacustrine-waxy claystone deposited in a lake, but fossils n1ay be younger mixed in following lake recession.

hibits retention of the impression. High sedi111entation rate and frequent flooding events increase the potential for print preservation, because fresh prints are covered and buried before extensive modification can occur. Finally, Iin1ited post-depositional modification, for example co1npaction, increases the likelihood of preserving delicate structures, such as invertebrate trace fossils or human footprints (Leakey and Hay, 1979).

In summary, ideal conditions for recording individual footprints and trails are moderately moist, silty sediments, with a low rate of animal activity (trampling) relative to rate of sedimentation (Fig. 8). Covering the sedimentary structure quickly and having minimal post-depositional compaction enhances preservation potential. Well-preserved footprints are relatively rare in the geological record of wet1ands, whereas massive sediments are more co1nmon. Thus, the long term picture within a wetland is one typified by relatively low energy, fluctuating water availability and a high rate of trampling relative to the rate of seditnentation.

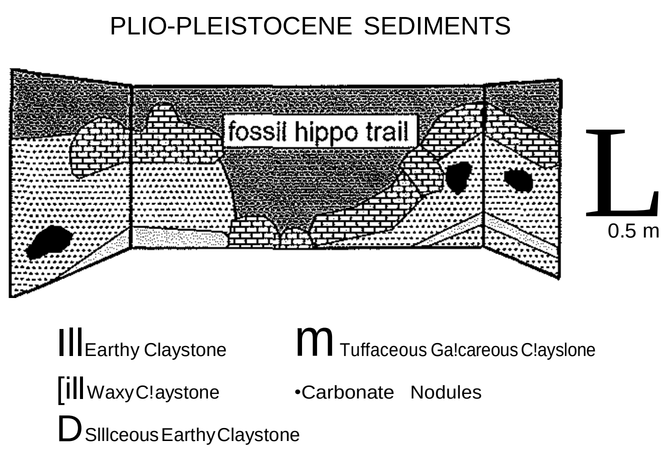


FIG. 7. Ancient hippo trail (1.75 million years old). An excavation exposes lake-margin stratigraphy of interbedded waxy claystone, earthy claystone and tuffaccous claystone. Carbonate deposits were found nearby indicating a spring or groundwater seep. A U-shaped depression (1.2 m wide and 60 cm deep) is eroded into the sediments. The depression was later infilled by earthy claystone. Based on modern analogs, this depression is interpreted as a hippo trail.

Paleoecological Implications

Hippos *(Hippopotamus amphibius)* are important to the ecology of permanent wetlands in Africa and have significant environmental impact (Olivier and Laurie, 1974). They have been known to affect drainage avulsions in the Okavango Delta, Botswana and Ngorongoro Crater, Tanzania, by creating incised channels during daily excursions from permanent deep water pools used during the day to adjacent grazing areas utilized at night (McCarthy et al., 1998; Deocampo, 2002b). These trails lead away from the wetlands and criss-cross adjacent terrain (Fig. 5C, D). They represent significant topography in this otherwise flat tenain. They can be np to a few km long and range between 0.5 and 1 m wide and 0.5 to 1 m deep-much deeper, narrower, and straighter than one would expect fro1n a fluvial incision.

The trough exposed at Olduvai (Fig. 7) is similar in shape, scale, and context to hippo trails co1nmonly found at modern water holes (Deocampo and Ashley, 1997; McCarthy et al., 1998; Deocampo, 2000) (Fig. 5B,C, D). To our knowledge this is the first hippo track to be documented in Plio-Pleistocene sediments.

Modern hippos may well be occupying the same ecological niche and expressing similar behavior of an extinct group of large ve1tebrates, the amynodonts, that evolved in North America and later spread into Europe and Asia (Colbert, 1969). *Amynodon* (Eocene) and *Metamynodon* (Oligocene) were large, heavy vertebrates with short, broad feet and are fre-

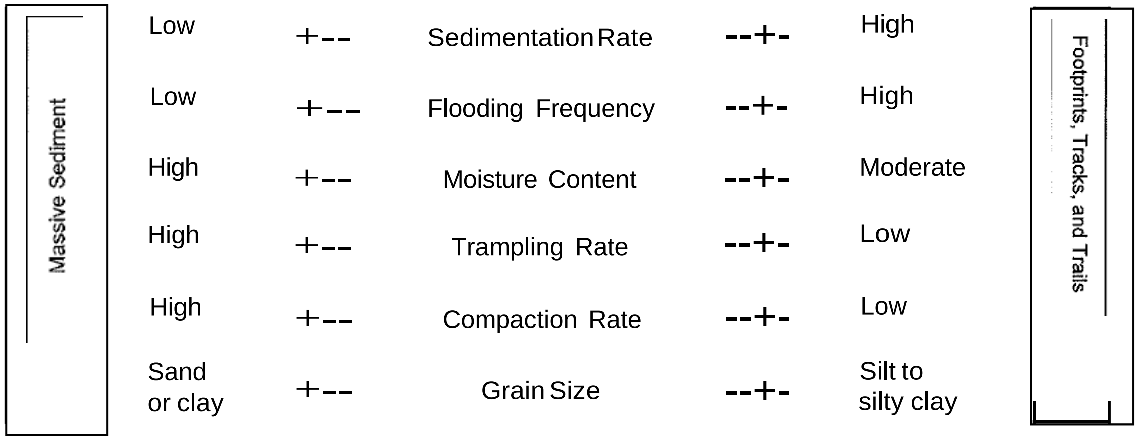


FIG. 8. Environmental factors that affect the nature of a vertebrate bioturbation record in groundwater-fed wetlands

quently found in stream-channel deposits, indicating that they may have been water-lovers like the modern hippopotamus.

Unusually naITow (1-2 m) and lm deep incisions in river channel banks and levees have been noted in the 55 Ma Lower Eocene Willwood Formation (in the Big Horn Basin, Wyoming) and are difficult to interpret in terms of natural fluvial processes (M. J. Kraus and. A. J. Pulham, pers. comms.). These incisions could represent trails of large vertebrates moving to and from the river channel and sources of food. *C01)71!10don*, a large pig or hippo-like n1ember of an extinct group kno\vn as pantodonts, had a herbivorous diet and would have been at home in swampy habitats (Rose, 2001). Ithad tusk:like canines and broad, crested molars to feed on vegetation, and is a reasonable ancient analog for the Plio-Pleistocene hippos at Olduvai and modern hippos at Ngorongoro Crater, Tanzania.

CONCLUSIONS

1. Groundwater-fed wetlands are lo\v energy environ111ents where the physical record appears to be dominated by biological processes. Sedimentation rates are generally lo\v and plant and animal activity relatively high.
2. The wetland bioturbation record reflects a number of interacting factors, such as substrate texture, moisture content, sedimentation rate, frequency of flooding, types and numbers of aniinals present, trampling rate, and post-depositional changes (compaction).
3. Organic-rich wetland sediments in se1ni-arid regions may oxidize and thus all that remains are vestiges of the former habitat: localized carbonate and diatomite deposits, sandy and silty claystones, and siliceous earthy claystones containing plant remains, bone frag1nents, pollen, and phytoliths. Vertebrate bioturbation leaves a physical record that can provide indirect information on the ecology of the paleoenvironment despite the loss of organic remains.
4. The impact of large mammals on the wetland sediment record is pervasive and ranges from thoroughly bioturbated sediments pummeled by thousands of hooves to trails of superimposed tracks and discrete footprinted surfaces.
5. A paleo hippo trail (1.2 m wide and 0.6 m deep) was interpreted in the Plio-Pleistocene wetland deposits based on comparison to modern analogs.
6. Preservation potential of the massive bedding (intense trampling) is excellent and is likely to occur in most circumstances. Ho\vever, preservation of footprints or trails requi.Tes a rapid burial to record the "snapshot in time." Dramatic change in sedimentaty regime occurs rarely in \vetland environments, particularly those isolated fro1n rivers or lakes.

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